Recent progresses in muricid shell studies: challenge and future works

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ABSTRACT   Numerous muricid shells have been described but unfortunately, the descriptions are often unsufficiently accurate to clearly characterize their diversity. This kind of imprecision is added to the morphological variation and increases the difficulty to classify them correctly. The traditional descriptive method has been reconsidered in the nineties and methodological progresses of comparative morphology were realized to perform muricid shell descriptions. They particularly concern the study of sculptural characters, for which structural homologies have been identified. After a historical analysis of the descriptive method from the 18th century until now, the interest of these progresses for phylogenetic and evolutionary approaches of the family is discussed. In this way, ontogenetic heterochronies in primitive muricids from the Lower Palaeogene (*Poirieria* and *Paziella*) and cladograms using shell characters are presented. The results using a performed descriptive method are promising, but still remain scarce. Perspectives for new works are given as an attempt to increase the relevance of these first results, while the references to the 80 studied or described species thanks the new descriptive method is listed.

RIASSUNTO   Una delle principali caratteristiche dei Muricidae è la presenza di un'elevata diversità morfologica nella scultura della conchiglia, acquisita nel corso della radiazione adattativa del gruppo, dal Campaniano-Maastrictiano fino ad oggi. Questa diversità è particolarmente evidente nelle corde spirali, che possono variare in numero, ordine di apparizione, distribuzione lungo la conchiglia, morfologia e tipo di proiezione (spine, noduli, etc.), offrendo un carattere importante ai fini della comprensione dell'evoluzione di tutta la famiglia. Sfortunatamente, nel passato, molte specie non sono state descritte con sufficiente precisione ai fini di una chiara caratterizzazione della diversità morfologica del gruppo, introducendo così una notevole confusione. Questo tipo di imprecisioni, unitamente alla straordinaria variazione morfologica dell'ornamentazione, rende ancora oggi molto arduo il compito di delineare una corretta classificazione dei Muricidae. Tuttavia, a partire dagli anni novanta, grazie al fiorire degli studi di morfologia comparativa, sono state riconosciute nella scultura delle conchiglie dei muricidi alcune omologie strutturali; con questo tipo di informazione, unitamente ai classici metodi descrittivi tradizionali, è oggi possibile formulare nuove ipotesi di lavoro attingendo quindi da entrambi i campi. Nel presente contributo viene presentata una summa delle conoscenze morfologico descrittive relative al gruppo, a partire dal XVIII secolo fino ad oggi, ed i cladogrammi più recenti ottenuti dallo studio di caratteri morfologici, anatomici o molecolari vengono commentati. Inoltre, è applicato un nuovo metodo descrittivo di classificazione dell'ornamentazione basato su due stadi di analisi dei cordoni spirali: dapprima si stabilisce la corrispondenza ontogenetica degli stessi e, solo successivamente, la loro corrispondenza topologica. Con questo nuovo metodo, grazie alla standardizzazione della terminologia da usarsi per definire strutture omologhe, è possibile sia una descrizione oggettiva dell'ornamentazione longitudinale, sia la comparazione di questo tipo di scultura tra specie diverse. Il nuovo metodo è stato applicato a circa 80 specie di Muricidae sia viventi che fossili, riguardo alle quali vengono riportati i riferimenti bibliografici. Riguardo ad alcuni muricidi primitivi appartenenti ai generi *Poirieria* e *Paziella*, vengono anche illustrate e discusse alcune eterocronie ontogenetiche. I risultati ottenuti con il nuovo metodo descrittivo appaiono, nel complesso, molto promettenti anche perché consentono un'integrazione del dato paleontologico con quello zoologico; tuttavia, appare chiaro come molte più specie debbano essere prese in considerazione e molto altro lavoro resti ancora da fare prima di poter dare enfasi a questo tipo di approccio.

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INTRODUCTION

One morphological characteristic of the muricid radiation (Campanian-Maastrichtian to Recent) is the high sculptural diversity, probably the highest in the Gastropoda, which illustrates its evolutionary importance for the family. This diversity is particularly expressed in the spiral cords and is easily recognizable through a variation of their number, order of appearance, distribution along the shell, morphology, and types of axial projection (spines, nodules). In comparative morphology, the muricid spiral sculpture corresponds to a serial homology, and following the definitions of Grandjean (1943) and Bouligand (1989), it may be placed between a « cosmiotaxic » group and an « orthotaxic » group, because the number of the cords is variable but limited. Nevertheless, the descriptive method was only able to count the number and the morphology of these cords, but did not consider which cord (s) change (s) from a species to another one. Therefore, the evolutionary modifications of the spiral sculpture remain unstudied and are still poorly known, the concept of homology in this character complex being very narrow. After a historical review of the method used to describe muricid shells, several recent results integrating the concept of homology will be discussed to delineate future challenges and perspectives.

ABBREVIATIONS

Descriptive text-conventions (Merle, 2001): P: primary cords (= cords appearing in first order); IP: infrasutural primary cord; P1: shoulder cord; P2 to P6: primary cords of the convex part of the whorl; ADP: adapertural primary cord on the siphonal

canal; MP: median primary cord on the siphonal canal; ABP: abapertural primary cord on the siphonal canal; s: secondary cords (= cords appearing in second order).

Repository: IRSNB: Institut royal des Sciences naturelles de Belgique, Bruxelles; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, USA; RMNH: Nationaal Natuurhistorisch Museum, Leiden.

I - The decrease of the shell interest in the muricid classification

The muricids have long been appreciated by Venus for her hair's beautifulness, by the Romans and other people for the purple dye, by the collectors for their attractive shells, and together with the cowries, cones, volutes and olivids are one the most emblematic family of the gastropods. No surprise, the muricid taxonomy starts with Linné who described the first taxa including many species, now attributed to various other families. Presently, about 2500 fossil and Recent species are recorded, showing the high diversity of the family. For a long time, the shell only was commonly used to distinguish the different muricid taxa. This practice prevailed without clear reservations, until the seventies when RADWIN & D'ATTILIO (1971), in a malacological congress, demonstrated that the members of the new subfamily Muricopsinae Radwin & D'Attilio, 1971 (e.g. *Muricopsis*, *Murexsul* and *Favartia*), whose shell morphology resembles the several Muricinae (eg. *Hexaplex*), anatomically differ from them by their radular characters. In the same congress, Vokes (1971), the leading specialist of fossil muricids, presented a palaeontological hypothesis about the lineages studied by Radwin & D'Attilio. She was amazed by the divergence of the conclusions using shell *versus* radula, but she accepted that anatomical results may be more pertinent at subfamilial level. Consequently, the radula soon became the most widely used character complex to distinguish subfamilies among the muricids (KURODA & HABE, 1971; RADWIN & D'ATTILIO, 1978; FUJIOKA, 1985; KOOL, 1987; HOUART, 1994a, b, 1995; BOUCHET & HOUART, 1994, 1996).

Although the radula, in numerous cases, allows to correctly classifying muricids in the ten recognized subfamilies, the evolution did not generate nine sufficiently different radula morphologies to always clearly discriminate them. Moreover, several highly derived radulae [e.g. *Drupina* (Rapaninae) and *Typhisopsis* (Typhinae)] or a total loss of radula (e.g. Coralliophilinae) cannot be referred to a particular subfamily without considering shell morphology as well. Therefore in many works, the shell was used in association with the radula in order to distinguish muricids subfamilies. Nevertheless, KOOL (1993b), studying the rapanine phylogeny, strongly criticised this practice and considered that the shell is *"the root of the taxonomic discord"*. It is true that before Kool, the previous classifications of the Rapaninae, using mainly the shells, radula and operculum, comprise polyphyletic or paraphyletic assemblages. In addition, the Rapaninae have been excluded of the muricid family in several semi-popular works (RADWIN & D'ATTILIO, 1976; FAIR, 1976). Following Kool, numerous shell variations and morphological convergences are the source of taxonomic mistakes and generate a loss of resolution of the phylogenetic trees. Consequently,

anatomical characters should be regarded as the most fruitful way for phylogenetic investigations and for an accurate muricid classification. Although the Kool's conception should not be neglected, it causes a real syndrome for a holistic approach of the muricid radiation, because it clearly excludes the fossils. In other words, about 80 millions years of biological evolution and more than 1000 species would be overlooked! The Kool's conception is derived from the cladistic (or hennigian) revolution, but a historical analysis demonstrates that the muricid shell descriptions were not adapted to this revolution, the concept of homology being too narrow.

II - Historical outline of the muricid shell descriptions until 1990

As consequence of the stratigraphic range of the muricid radiation, their shells have been described by both palaeontologists and zoologists. The aim of these works was mainly the identification of the taxa at different hierarchic levels and the external shells were systematically described, yet more or less accurately. However, a close analysis of the publications demonstrates that there is no major difference between the muricid teleoconch descriptions of the 19th century and these of the end of the 20th century. For example, the descriptions of the Eocene teleoconch muricids from Gan (MERLE 1990) are not really more precise, than those of DESHAYES (1835, 1865) for the Eocene muricids from the Paris basin. Regarding the homology, only the shoulder cord (P1) has been usually clearly identified by the authors, because it is widespread and often well marked on the shells. The papers by VIGNON (1931a, b) need to be mentioned here, because they demonstrate that two types of labral spines may be distinguished, the cord spines and groove spines. Nevertheless, these characters are too restricted to be useful for the entire family.

During the 20th century, three descriptive progresses have been developed. The most widely used in the description results from ontogenetic studies, and give much weight to the fact that the protoconchs may allow identifications at specific level for many marine gastropods, including the muricids (HOUART, 1989). The interest for the protoconch comes from the presence of two types of larval development (planktotrophic and lecithotrophic), which indicate different species, when even their teleoconch characters look similar. In addition, observations of the protoconchs are easy on preserved specimens, and need no expensive technology. However, if the protoconch may be very useful at specific level, it also represents a phylogenetic pitfall, because it is highly homoplastic (BOUCHET, 1983, 1987). Effectly, the acquisition of a lecithotrophic protoconch from an ancestor having planktotrophic protoconch is often observed in different lineages of the family.

The second method, less used in the descriptions, is the analysis of the microstructure. The muricid microstructure is mainly composed of aragonitic layers, but in several groups (Rapaninae, Ocenebrinae and Trophoninae) an external calcitic layer may occur. PETITJEAN (1965) extensively studied the microstructure of fossil and recent species, and KOOL (1993b) pointed out its interest in his phylogenetic study of the Rapaninae.

The third descriptive progress concerns the superficial microstructure generating a peculiar microsculpture, termed as

intritacalx. This method has been developed by D'ATTILIO & RADWIN (1971), who demonstrated the interest of the intritacalx for identifications at the specific level in different muricids, such as the Typhinae and the Muricinae (eg. *Aspella*).

Finally, except for the considetation of the protoconchs, the microstructure and the intritacalx, the method of shell description remained unchanged and the concept of homology only made a few incursions in the study of the sculptural elements until the end of the 20th.

III - The rise of the concept of homology in the muricid shell descriptions

Curiously, the first introduction of the concept of homology in the descriptions of the muricid spiral sculpture did not come from the cladistic revolution or from evolutionary studies. In fact, it came from identification problems. HYLLEBERG & NATHEEWHATANA (1992) first pointed out these problems and wrote that many descriptions cannot allow a correct determination of taxa (species). When studying the Recent *Chicoreus ramosus* (Linnaeus, 1758), they gave a closer description, attempting to homologise each cord spine by using the topological correspondence of the spiral alignments. This way was also used by DE VRIES (1997) in a study of American fossil and Recent species of the genus *Chorus*, for which each cord of several species has been depicted. The topological correspondence of the cords has also been used by VERMEIJ (1995). Following the cladistic work by KOOL (1993b) on the Rapaninae, Vermeij discussed the subfamilial position of the fossil genus *Ecphora*, identified the subsutural cord (SP) and demonstrated that it is widespread in the Rapaninae, while it is absent in the Ocenebrinae. Nevertheless, if the search for the topological correspondence is an accurate approach to identifying characters among the spiral sculpture, which is already used for several holostomatous gastropod families [Calliostomidae (Marshall, 1995), Mathildidae (Bieler, 1995), Architectonicidae (Bieler, 1988) and Turritellidae (Allmon, 1994)], it is not sufficient for two reasons. Firstly, the appearance of the muricid cords is organized in different sequences. Secondly, the intensity (the relief) of the development of the cords may change during shell growth. Therefore,
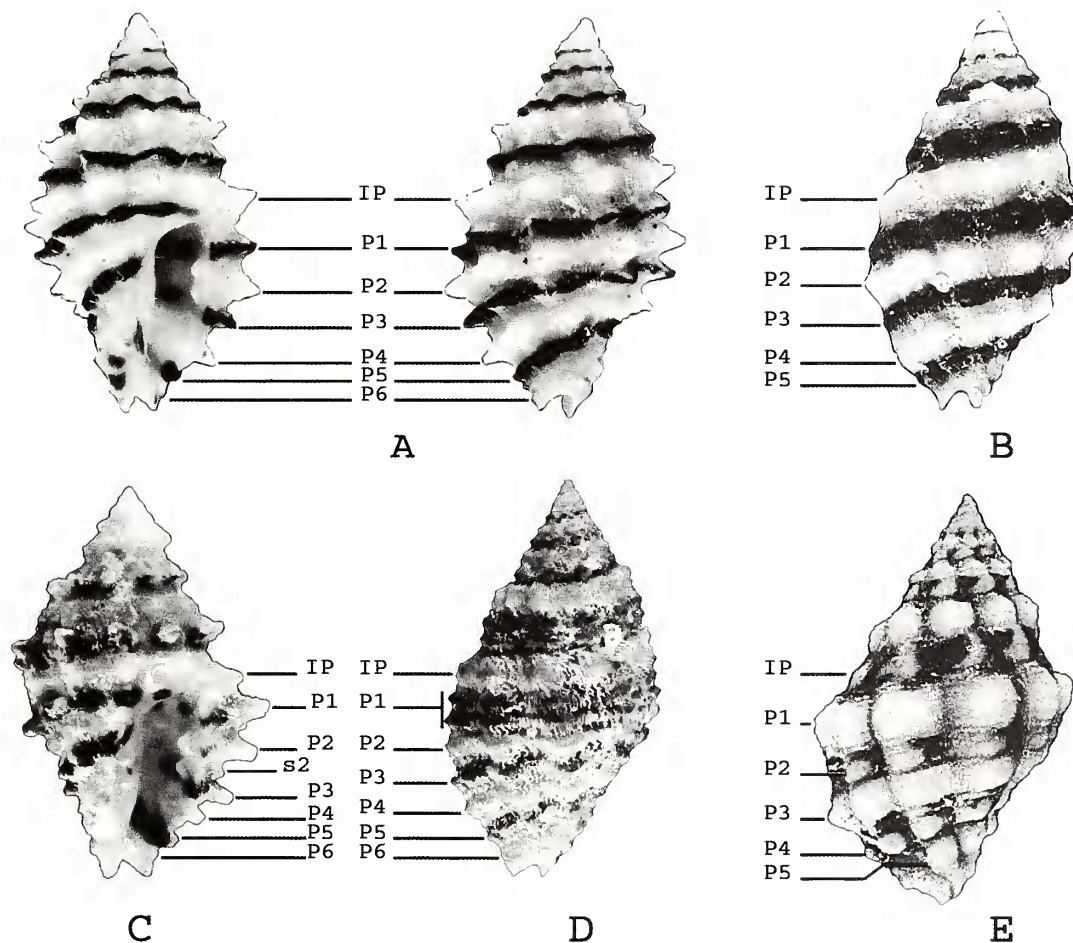

Fig. 1: A: *Morula albanigra* Houart, 2002, Guam lagoon, holotype IRSNB IG29532, H: 7.5 mm (ventral and dorsal views); B: *M. nodicostata* (Pease, 1868), French Polynesia, Tahiti, R. Houart coll., H: 6.4 mm (dorsal view); C: *M. cernohorskyi* (Houart & Tröndle, 1997), Tuamotu Archipelago, Mururoa atoll, paratype R. Houart coll., H: 5.8 mm (ventral view); D: *Morula parva* (Reeve, 1846), Indonesia, Ambon, S.E. side of Pombo Island, RMNH, H.: 8.5 mm (dorsal view). Note that the P1 cord is split; E: *M. variabilis* (Pease, 1868), French Polynesia, Paumotus (Tuamotu), lectotype MCZ 260618, H: 6.9 mm (dorsal view).

Fig. 1: A: *Morula albanigra* Houart, 2002, laguna di Guam, olotipo IRSNB IG29532, H: 7.5 mm (vista ventrale e dorsale); B: *M. nodicostata* (Pease, 1868), Polinesia Francese, Tahiti, coll. R. Houart, H: 6.4 mm (vista dorsale); C: *M. cernohorskyi* (Houart & Tröndle, 1997), Arcipelago delle Tuamotu, atollo di Mururoa, paratipo, coll. R. Houart, H: 5.8 mm (vista ventrale); D: *Morula parva* (Reeve, 1846), Indonesia, Ambon, lato SE dell'Isola di Pombo, RMNH, H.: 8.5 mm (vista dorsale). Notare la divisione della corda P1; E: *M. variabilis* (Pease, 1868), Polinesia Francese, Paumotus (Tuamotu), lectotipo MCZ 260618, H: 6.9 mm (vista dorsale).

the possibilities of mistakes in the identification of the cords greatly increase without reference to ontogeny. This has been documented in several articles (MERLE, 1999, 2001; MERLE *et al.* 2001), stressing that muricid primary cords (cords of the first sequence of appearance) may have a small relief, similar to that of the secondary cords, in the end of the growth and, conversely, that secondary cords may have a strong relief, similar to that of the primary cords. Finally, the adopted methodology to identify more accurately spiral cords and thus their structural homologies, was a combined research of their ontogenetic and their topological correspondences. It consists of detecting the ontogenetic correspondence in a first step of the analysis, and the topological correspondence in a second step. Then, a standard terminology of the structural homologies has been established for each major sequence of appearance (primary and secondary cords), using the maximum number of topological positions retrieved in the youngest most ornamented muricids (MERLE, 1999, 2001).

The authors (Houart and Merle) have changed their descriptive habits since 1999, as they became convinced that researches of structural homologies through the spiral sculpture was one of the necessities of comparative morphology for a better evaluation of the muricid radiation (evolutionary and phylogenetic aspects). In particular, they used the standard terminology and, for a clear presentation of the characters, the identified homologies have been shown in figures. This new presentation is made with respects to the observations of HYLLEBERG & NATHEEWHATANA (1992), who stressed that it was often impossible to recognize the characters in the descriptions and also because, in comparative morphology, each
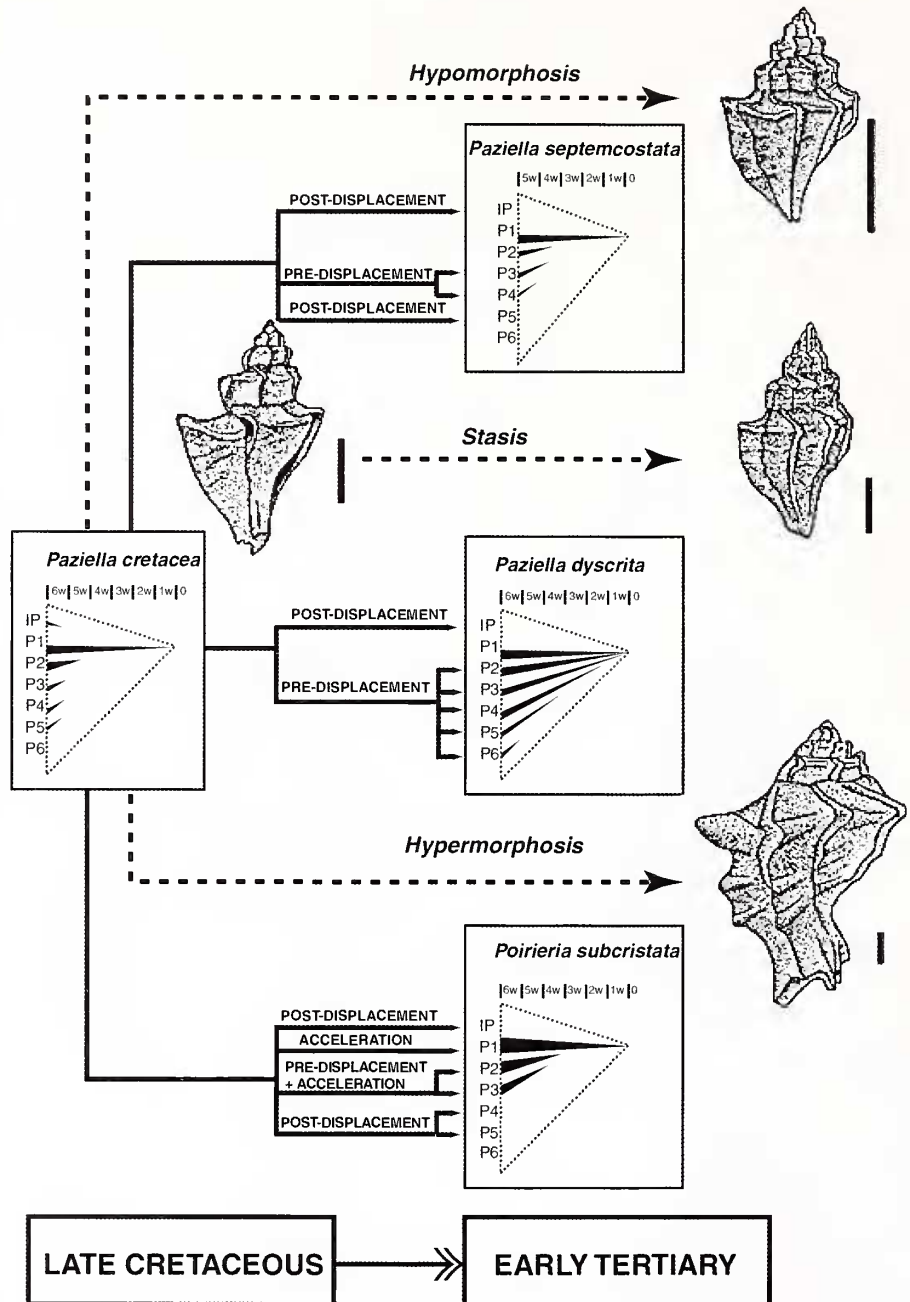

Fig. 2: Possible ontogenetic heterochronies of the primary cords in the Palaeocene and Lower Eocene muricids (*Paziella* and *Poirieria*) after Merle & Pacaud (2002) modified. *Paziella cretacea* (Garvie, 1991) (Campanian-Masstrichtian from Texas, USA) is chosen as a primitive morphological reference. In *Paziella septemcostata* (Rouault, 1850) (Upper Ypresian from the Aquitaine basin), the small pre-displacement of P3 and P4 associated with a hypomorphic shell; IPC and P5 are post-displaced. In *Paziella dyscrita* (Cossmann, 1889) (Upper Ypresian from the Paris basin), IPC is post-displaced while P2 to P6 are predisplaced. In *Poirieria subcristata* (Lower Ypresian from United-Kingdom), the acceleration of P1, the acceleration and the predisplacement of P2 and P3, and the post-displacement of IPC, P4 and P5 are asociated with a hypermorphic shell. Scale bar = 5 mm.

Fig. 2: Possibili eterocronie ontogenetiche nei cordoni primari dei muricidi del Paleocene ed Eocene Inferiore, generi *Paziella* e *Poirieria*; modificato da Merle & Pacaud (2002). *Paziella cretacea* (Garvie, 1991) (Campaniano-Maastrichtiano del Texas, USA) è presa in considerazione come modello di morfologia ancestrale. In *Paziella septemcostata* (Rouault, 1850) (Ypresiano Superiore del Bacino Aquitaniano), è possibile osservare un fenomeno di ipomorfosi, con semplificazione della scultura della conchiglia; i cordoni primari P3 e P4 si possono osservare solo a partire dal quarto giro; la corda infrasuturale IP ed il cordone primario P5 non compaiono. In *Paziella dyscrita* (Cossmann, 1889) (Ypresiano superiore del Bacino di Parigi), i cordoni primari da P2 a P6 compaiono già nei primi giri, mentre IP è assente. In *Poirieria subcristata* (Ypresiano inferiore del Regno Unito), l'ingrossamento di P1, l'ingrossamento unito ad una comparsa precoce di P2 e P3, e l'assenza di IP, P4 e P5, caratterizzano una conchiglia dalla scultura molto più evidente e rilevata (ipermorfia). w = giro di spira. Scala di riferimento = 5 mm.

character must be clearly illustrated to be discussed. The list of the species figured in the publications is given (Appendix 1). It may constitute a first database on the subject. This list includes 81 species (19 fossil and 62 Recent) for 37 genera and subgenera. Twenty two type-species are also illustrated. Five *Morula* species (Rapaninae) commented upon by HOUART (2002b), but not illustrated, are figured here (Fig. 1A-E).

IV -Evolution of the primitive muricids

The oldest known muricid is *Paziella cretacea* (Garvie, 1991) from the Campanian-Maastrichtian of Texas (Kemp Clay). *Paziella* is not yet recorded in the Upper Maastrichtian, but it occurs together with *Poirieria* and *Pterynotus* in the Early Tertiary beds of the Danian. The *Paziella* and *Poirieria* species from the Palaeocene and the Lower Eocene received a special attention, because, according to several authors (VOKES, 1992; PONDER & VOKES, 1988; HARASEWYCH, 1984), on the basis of the argument of geological precedence, they are assumed to represent the most primitive muricids. Therefore, their sculptural pattern needed to be closely examined for a better understanding of the later sculptural changes observed in the muricid radiation. Moreover, a detailed inspection of these shells using structural homologies of the spiral sculpture represents one of the keys for phylogenetic analyses including fossils, *Paziella* and *Poirieria* being be regarded as potential outgroups. The studies using *Paziella* and *Poirieria* allow considering four results about the evolution of primitive muricids.

1°) Paziella as a survivor of the K/T crisis

The comparison between *P. cretacea* and the Early Tertiary species of *Paziella* (MERLE & PACAUD, 2002a), does not reveal significant sculptural changes, except for the loss of fine columellar denticles. The few transformations suggest that the Early Tertiary *Paziella* species clearly derive from a Cretaceous stock surviving after the K/T crisis.

2°) Primitive muricids: a poorly developed spiral sculpture

The ontogenetic observations emphasize that *Poirieria* and *Paziella* share a low development of their spiral sculpture (MERLE & PACAUD, 2002a, b). Young specimens are particularly unornamented and only possess one to three primary cords (P1 to P3 on the two early whorls). During the growth, several other primary cords appear abapically (P4, and P5 and P6 in *Paziella*), but the siphonal canal always remains unornamented (ADP, MP and ABP are missing) (Fig. 2).

3°) Rule of heterochronies in early sculptural changes

The sculptural variations of Lower Eocene and Paleocene *Poirieria* and *Paziella* species may be interpreted as the result of ontogenetic heterochronies (MERLE & PACAUD, 2002a, b). Morphologies that are affected by paedomorphoses tend to have a less developed sculpture (fewer cords with a later appearance) than in *P. cretacea*. Conversely, morphologies affected by peramorphoses tend to have a more developed sculpture (more numerous cords with an earlier appearance) than in *P. cretacea* (Fig. 2).

4°) Sculptural contrasts between early and modern tropical muricids

The sculptural patterns of the Palaeocene and Lower Eocene *Poirieria* and *Paziella* species contrast with those of modern tropical muricids {eg. *Siratus*, *Murex* in the Muricinae or *Favartia*, *Murexsul* in the Muricopsinae (HOUART 2000, 2001a, b, 2002a; HOUART & DHARMA 2001; MERLE, 1999, 2002; MERLE *et al.*, 2001)} in which the sculptural elements become more numerous, more developed and more diversified. Conversely, there is not a great sculptural contrast between the primitive muricids and deep or coldwaters muricids.

V - Congruences with biological studies

We analyse here, the congruences between three phylogenetic trees based on shell characters (MERLE 1999, 2002; VERMEIJ & CARLSON 2000) and trees based on anatomical or molecular characters. The first phylogeny (MERLE, 1999) is focused on the Muricopsinae, but includes various members of other subfamilies (Rapaninae, Ergalataxinae, Ocenebrinae, Trophoninae, Typhinae, Tripterotyphinae and Muricinae) (Fig. 3A). The second one (VERMEIJ & CARLSON, 2000) is focuses on the Rapaninae and includes the Ergalataxinae, Ocenebrinae and one species of Muricinae. The third one (MERLE, 2002) concerns the Muricopsinae and several members of the Muricinae (Fig. 3B). In the first and the third phylogenies, structural homologies based on the analysis of the spiral sculpture are used.

1°) Rapaninae/Ergalataxinae

The rapanine phylogeny has been studied by KOOL (1993b) who used anatomical characters. He demonstrated that *Stramonita* and *Drupa* belong to the clade Rapaninae, while *Nucella* is excluded and belongs to the clade Ocenebrinae (Fig. 3C). The results of MERLE (1999) also concluded to distinguish the two clades, but suggested that the Ergalataxinae *Orania* is more closely related to the Rapaninae than to other taxa. The cladogram of VERMEIJ & CARLSON (2000, fig.1) shows a node (node T) in which *Stramonita* and *Drupa* are grouped, but in the node E several Rapaninae (eg. *Cymia*) are included with ergalataxine taxa (eg.: *Ergalatax*, *Cronia* and *Muricodrupa*). In this cladogram, the distinction between the Ocenebrinae and Rapaninae is not clear and *Nucella* cannot be discussed because it is regarded as outgroup. Despite some problems concerning the Ocenebrinae in the phylogeny of VERMEIJ & CARLSON (2000), many rapanine taxa are grouped in a same clade. Moreover, both phylogenies based on shells suggest possible relationships between the Ergalataxinae and the Rapaninae. As Vermeij & Carlson (2000) wrote, the ergalataxine systematics should be re-analysed in order to define their relationships with the rapanine radiation.

2°) Ocenebrinae/Trophoninae

The phylogenic relationships of some ocenebrine taxa have been studied by KOOL (1993a, b) using anatomical characters and by MARKO & VERMEIJ (1999), OLIVERIO & MARIOTTINI (2001), OLIVERIO *et al.* (2002) using molecular data. Kool's tree (1993a, fig. 65) suggests that *Nucella* and *Ocenebra* are more closely related with *Trophon (s.s.)* than with the Rapaninae (Fig. 3D). This result is found in Merle's tree (Fig. 3A), which only differs from Kool's tree one by the position of *Trophon (s.s.)*, which is more closely related to *Nucella*. Moreover, the position of *Forreria* in the Ocenebrinae is also suggested in the Kool's (1993b) and Merle's (1999) trees. Regarding the relationships of the Ocenebrinae among the Muricidae, OLIVERIO *et al.* (2001) suggested that the Ocenebrinae (represented by *Nucella* and *Ceratostoma*)
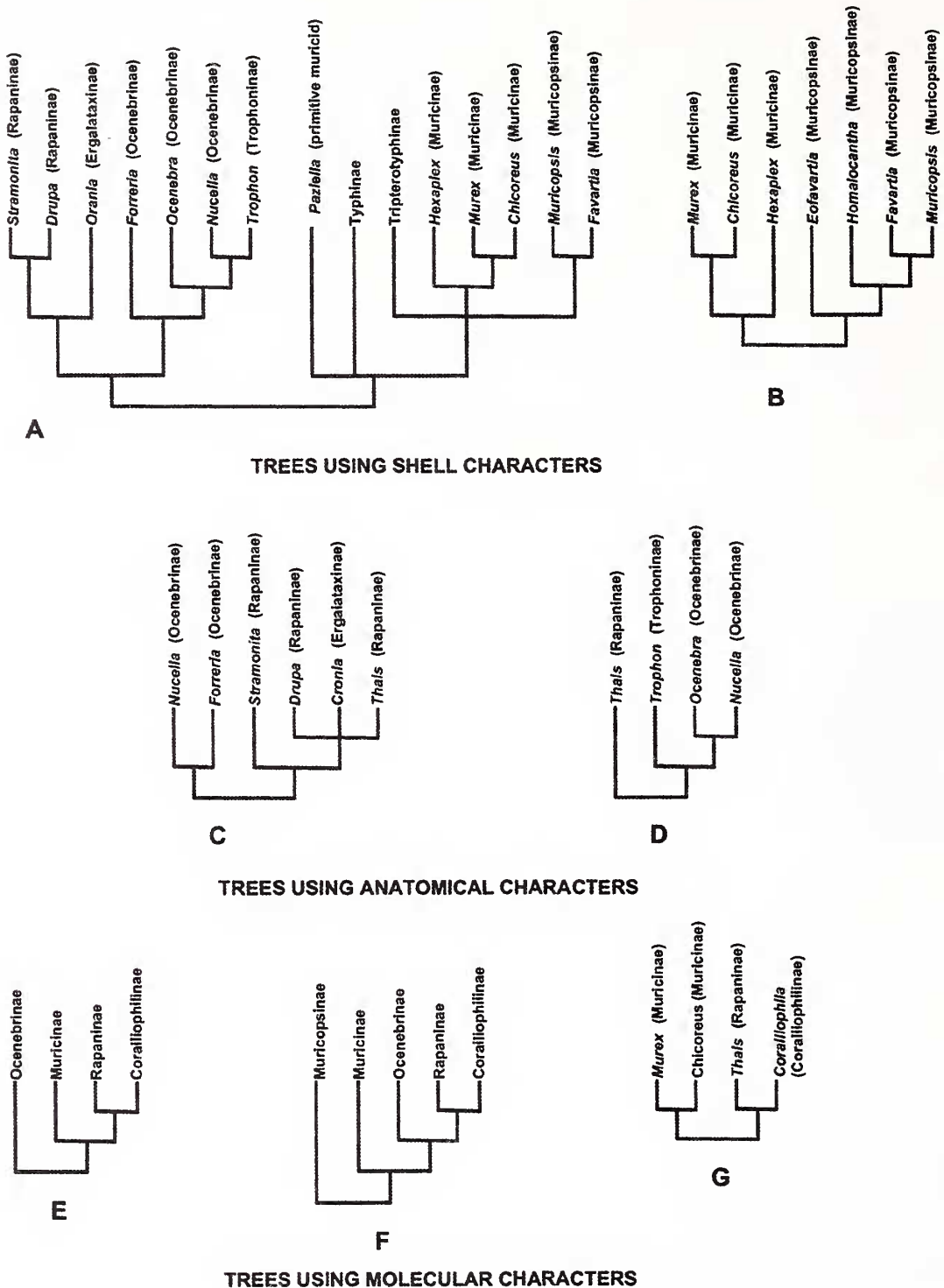
TREES USING SHELL CHARACTERS

TREES USING ANATOMICAL CHARACTERS

TREES USING MOLECULAR CHARACTERS

Fig. 3: Comparisons between trees using shell (A-B), anatomical (C-D) and molecular (E-G) characters. **A**: synthetic tree of MERLE (1999, figs 86 and 87); **B**: tree of MERLE (2002); **C**: tree of KOOL (1993b) only considering the taxa studied by MERLE (1999), with *Cronia* (Ergalataxinae) and *Thais* (Rapaninae) to show the possible relationships between the Ergalataxinae and the Rapaninae; **D**: tree of KOOL (1993a); **E**: tree of OLIVERIO & MARIOTTINI (2001); **F**: tree of OLIVERIO *et al.* (2002) (preferred hypothesis); **G**: tree of HARASEWYCH *et al.* (1997).

Fig. 3: Comparazione tra alberi ottenuti utilizzando caratteri conchigliari (A-B), anatomici (C-D) e molecolari (E-G). **A**: albero sintetico di MERLE (1999, figs 86 and 87); **B**: albero da MERLE (2002); **C**: alberodi KOOL (1993b) ottenuto considerando solamente i taxa studiati da MERLE (1999), unitamente a *Cronia* (Ergalataxinae) e *Thais* (Rapaninae) al fine di evidenziare le possibili relazioni esistenti tra Ergalataxinae e Rapaninae; **D**: albero di KOOL (1993a); **E**: albero di OLIVERIO & MARIOTTINI (2001); **F**: albero di OLIVERIO *et al.* (2002) (ipotesi preferita); **G**: albero di HARASEWYCH *et al.* (1997).

may be regarded as a basal taxon whose sister-group is the clade: (Muricinae (Rapaninae, Coralliophinae)) (Fig. 3E). This result is not congruent with Merle's tree, which suggests that the clade Rapaninae/Ergalataxinae is more closely related to the clade Ocenebrinae/Trophoninae. However, in a subsequent phylogeny, OLIVERIO et al. (2002) suggested that the Ocenebrinae may be more closely related to the clade including the Rapaninae and the Coralliophilinae: (*Nucella* [Ocenebrinae] ((*Stramonita, Concholepas* [Rapaninae]) *Coralliophila* [Coralliophilinae])) (Fig. 3F).

3°) Muricinae

In their phylogeny of the Neogastropoda based on the cytochrome *c* oxidase I sequence, HARASEWYCH et al. (1997) include several Muricidae (*Murex, Chicoreus, Thais* and *Coralliophila*) (Fig. 3G). The resulting tree [fig. 6 = ((*Murex, Chicoreus*), (*Thais, Coralliophila*))] clearly suggests that *Murex* and *Chicoreus* are closely related, and the same result is found in Merle's trees (MERLE 1999, 2002) including *Hexaplex* [which is used as a muricine taxon in the tree of OLIVERIO et al. (2002)]. Regarding the relationships among the Muricidae, the hypothesis of OLIVERIO & MARIOTTINI (2001) is that the Muricinae is a basal taxon, whose sister-group is the clade: (Rapaninae, Coralliophilinae). In a further study, OLIVERIO et al. (2002) suggested that the Muricinae are more derived than *Muricopsis* (Muricopsinae) and is sister-group of the clade: (Ocenebrinae (Rapaninae, Coralliophilinae)), the entire tree being: (Muricopsinae (Muricinae (Ocenebrinae (Rapaninae, Coralliophilinae)))). This result differs from those of Merle, which suggests that the Muricopsinae are more closely related to the Muricinae than the other subfamilies (Fig. 3A- B), but both share the relatively close relationships between the Muricopsinae and the Muricinae (Fig. 3F).

4°) Muricopsinae

The Muricopsinae have been individualised from the Muricinae by radular characters (RADWIN & D'ATTILIO, 1971). Particularly, the *Muricopsis* group shares similar radular morphology with the *Favartia* group. For MERLE (1999, 2001, 2002), the Muricopsinae also differ from the Muricinae by derived shell characters and represents a clade with three main branches, the fossil *Eofavartia* branch, the *Favartia* branch and the *Muricopsis* branch.

Finally, it is a difficult exercise to compare the different phylogenetic trees because they often correspond to partial analyses of the family, but two points are evident. Firstly, very similar patterns are found for the members of a same subfamily (eg. Rapaninae (*Drupa* and *Stramonita*); Ocenebrinae (*Nucella, Forreria* and *Ocenebra*); Trophoninae (*Trophon* and the Ocenebrinae); Muricinae (*Murex, Chicoreus* and *Hexaplex*), as well in the trees based on shell data, as in the trees based on anatomical or molecular data. Second, the relationship between the Muricinae, the clade (Rapaninae, Coralliophilinae) and the Ocenebrinae is still not fully resolved in both approaches.

VI - Challenges for futur works

In 1992, Bieler wrote *"Gastropods have remained surprisingly under-utilised as models for and object of evolutionary studies. No other animal group offers equal opportunities to combine the findings of comparative morphological and molecular studies on diverse extant fauna with data derived of the extensive fossil record."* The muricids, with their Cenozoic diversification, numerous Recent species and a world-wide geographic range, perfectly illustrate Bieler's remarks, giving these equal opportunities for paleontologists and zoologists. However, they should not be too much disconnected to avoid that zoological studies ignore the temporal dimensions of the muricid radiation and that paleontological studies continue to consider the species as a simple collection of objects. The cladistic revolution, mainly based on anatomical investigations, questioned the informations of the shells (KOOL, 1993), but an answer is that the descriptive system of the shells was still in its childhood. The recent rise of the concept of homology in this system represents a step toward its maturity, but progresses which are challenges themselves are needed. For the next decades, three kinds of challenge may be outlined in order to obtain a holistic approach of the muricid radiation.

1°) Prolongation of the researches on shell homologies

The first priority is the prolongation of researches on the homologies. The appendix records about 80 Recent and fossil species in which sculptural homologies of the spiral sculpture are published and illustrated, but the family contains about 2500 species. It is still insufficient for a closer knowledge of the sculptural diversity and a database including about 500 species would be the needed for the start of a statistical approach. The search of the target taxa should be not exclusively oriented on the tropical species, which evolved quickly and bear spectacular patterns, but also should also consider cold and deep water species. Another way to perform the descriptive system in terms of homologies is the study of the constructional characters (MILLER, 1999; MILLER & MERLE, 2003), which is under-utilised, but may be applicable for a better approach of the axial sculpture.

2°) Evolutionary studies based on ontogeny

More or less spectacular changes of the spiral sculpture during growth have been described in the genera *Poirieria, Paziella, Chicoreus (Siratus), Murexsul* and *Xastilia* (MERLE, 1999, 2001; MERLE et al, 2001; MERLE & PACAUD, 2002a, b). They suggest the importance of the evolutionary studies based on ontogeny for the knowledge of the diversification. These studies are necessary to understand the different ways of sculptural change, which are known in few taxa. Regarding this problem, several questions remain unstudied. For example, how many change pathways are there in the muricids, and how environmental factors control them? In addition, the knowledge of these pathways is important in phylogenetic analyses, because it allows a better character coding.

3°) Phylogenetic analyses

Phylogenetic analyses of the Muricidae arose in the nineties. They are mainly based on anatomical or molecular data, and provided substantial progresses in the knowledge of the diversification and the classification. Particularly, the revision of the clade Rapaninae (KOOL, 1993a, b) and the placement of the Coralliophilidae in the muricid (now Coralliophilinae) as sister group of the Rapaninae (OLIVERIO & MARIOTTINI, 2001; OLIVERIO et al., 2002) need to be stressed. However, new progresses in this field are necessary because the phylogenetic relationships between the Muricinae, Ocenebrinae and the clade Rapaninae + Coralliophilinae are not fully resolved. Moreover, the relation-

ship between the Ergalataxinae and Rapaninae need to be elucidated; these of the primitive muricids (*Poirieria* and *Paziella*) attributed to the Muricinae, and of the Typhinae and Tripterotyphinae are still rarely considered; the current classification of the Trophoninae is regarded as a polyphyletic assemblage (VOKES, 1996a, b; VERMEIJ & VOKES, 1997) in which *Trophon* seems closely related to the Ocenebrinae, while only *Muricopsis* has been recently introduced in a molecular study in the Muricopsinae.

Despite these problems, numerous congruences between anatomical, molecular and shell based trees at subfamilial level suggest that this latter character complex is not devoid of phylogenetic informations, when analysed in details. Therefore, these positive results are encouragements for a better consideration of the shell in phylogenetic studies, for more numerous comparisons of the shell based trees with molecular and anatomical ones and for the inclusion of fossils in phylogenies. The inclusion of fossil taxa is important for a better knowledge of the muricid phylogeny, because, as in other zoological groups, it gives character associations lacking in the Recent (DONOGHUE *et al.*, 1989; JANVIER, 1991). Moreover, progresses in the analyses of the cladograms, such as the stratigraphic tests (WAGNER, 1995; SIDDAL, 1998; POL & NORELL, 2001; ZARAGUETA-BAGILS & LELIEVRE, 2001) allow a better evaluation of the congruences of the phylogenetic trees based on fossils.

CONCLUSION

The Muricidae, one of the most emblematic gastropod families class, was regarded as a well studied group, considering the number of described taxa. Also, few progresses in its classification was expected until the seventies. The situation changed when the spreading of radular studies and phylogenetic analyses based on anatomical or molecular data called into question the validity of the muricid classification, which was mainly based on the shell. Consequently, a reflexion on the usefulness of the shell was necessary and an emerging answer was that the traditional descriptive method was obsolete for phylogenetic or evolutionary approaches. Particularly, the sculptural diversication, a basical adaptive tendency of the muricid radiation was not acurately evaluated. The results presented here come from the recent use of the concept of homology for the description of sculptural characters and stress again the poor knowledge of the family, as to the shell characters, despite numerous descriptions. Nevertheless, the use of the concept of homology generates new perspectives of works oriented toward a holistic view of the Cenozoic muricid radiation, giving the opportunity to better combine paleontological and zoological results. Finally, although this family is emblematic for the gastropod class, many aspects of its biology remain unrecognized and numerous progresses may be expected.

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Appendix 1: List and informations on the species for which the ontogenetical and topological correspondences of the spiral characters (cords and internal denticles of the outer lip) has been illustrated.

Appendice 1: Lista, con relative indicazioni bibliografiche, delle specie per le quali è stata illustrata la corrispondenza ontogenetica e topologica dei caratteri della spira presi in considerazione nel corso del presente lavoro (cordoni longitudinali e denti interni del labbro esterno).

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
		Subfamily MURICINAE		
Poirieria levis Traub, 1979	Thanetian to Ypresian (Austria)	Merle & Pacaud (*Bayerische Mitteilungen*, 2002)	Pl.2 (figs.1-2)	1 young and 1 adult

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Poirieria subcristata (d'Orbigny, 1850)	Ypresian (England, France)	Merle & Pacaud (*Bayerische Mitteilungen*, 2002) Merle & Pacaud (*Tertiary Research*, 2002)	Pl. 2 (figs 3-4) Pl. 1 (figs 1-4)	1 young and 1 adult
Poirieria sp. (Vokes, 1992)	Danian (Alabama, USA)	Merle & Pacaud (*Bayerische Mitteilungen*, 2002)	Pl. 3 (fig. 1)	1 adult
Poirieria woodsensis Vokes, 1970	Thanetian (Alabama, USA)	Merle & Pacaud (*Bayerische Mitteilungen*, 2002)	Pl. 3 (fig. 2)	1 adult
Poirieria zelandica (Quoy & Gaimard, 1833)	Recent (New-Zealand)	Merle (*Novapex*, 2001)	Fig. 2B	1 adult
Crassimurex (s.s.) calcitrapa (Lamarck, 1803)	Lutetian (France)	Merle & Pacaud (*Bayerische Mitteilungen*, 2002)	Pl. 3 (figs 3-4)	1 young and one adult
Paziella cretacea (Garvie, 1991)	Campanian-Maastrichtian (Texas, USA)	Merle & Pacaud (*Tertiary Research*, 2002)	Pl. 3 (figs 1-2)	1 adult
Paziella dyscrita (Cossmann, 1889)	Ypresian (France)	Merle & Pacaud (*Tertiary Research*, 2002)	Pl. 2 (figs 1-9)	5 spm, young to adult
Paziella septemcostata (Rouault, 1850)	Ypresian (France)	Merle & Pacaud (*Tertiary Research*, 2002)	Pl. 3 (figs 3-10)	4 spm, young to adult
Paziella pazi (Crosse, 1869)	Recent (Florida, USA)	Merle (*Novapex*, 2001)	Fig. 10A, D	1 adult
?Paziella plini (de Raincourt, 1874)	Lutetian/Bartonian France	Merle (*Annales de Paléontologie*, 2003)	Figs 4,5	4 spm, young to adult
Flexopteron primanova (Houart, 1985)	Recent (Madagascar)	Merle (*Novapex*, 2001)	Fig. 9C	1 adult
Chicoreus (Siratus) cailleti (P. de la Saussaye, 1856)	Recent (French West-Indies)	Merle *et al.* (*Zoosystema*, 2001)	Figs 1A-D, 6G, 8C	4 spm, young to adult
C. (Siratus) perelegans (Vokes, 1965)	Recent (French West-Indies)	Merle *et al.* (*Zoosystema*, 2001)	Figs 2A-C, 6B, 8D	3 spm, young to adult
C. (Siratus) consuela (Verrill, 1950)	Recent (French West-Indies)	Merle *et al.* (*Zoosystema*, 2001)	Figs 2D, 3A, 6C, 8F	2 adults
C. (Siratus) ciboney (Clench & Farfante, 1945)	Recent (French West-Indies)	Merle *et al.* (*Zoosystema*, 2001)	Figs 3B-D, 6A, 8A	3 spm young to adult
C. (Siratus) articulatus (Reeve, 1845)	Recent (Porto-Rico)	Merle *et al.* (*Zoosystema*, 2001)	Figs 5A-B, 6D, 8E	2 spm, young and adult

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
C. (Siratus) formosus (Sowerby, 1841)	Recent (Haiti)	Merle *et al.* (*Zoosystema*, 2001)	Figs 5C-D, 6F	2 spm, young and adult
C. (Siratus) guionneti Merle *et al.*, 2002	Recent (French West-Indies)	Merle *et al.* (*Zoosystema*, 2001)	Figs 6F, 7A-B, 8B	2 spm, young and adult
C. (Siratus) hennequini Houart, 2000	Recent (Honduras)	Houart (*Novapex*, 2000a)	Fig. 16A, C, E	1 adult
C. (Siratus) bessei Houart, 2000	Recent (Honduras)	Houart (*Novapex*, 2000a)	Fig. 16B,D, F	1 adult
Chicoreus (s.s.) ramosus (Linnaeus, 1758)	Recent (Thailand)	Merle (*Novapex*, 2001)	Fig. 9A	1 adult
Chicoreus (Triplex) setionoi Houart, 2001	Recent (Arafura sea)	Houart (*Novapex*, 2001b)	Figs 1-2	2 adults
Chicoreus (Triplex) longicornis (Dunker, 1864)	Recent (Australia)	Houart (*Novapex*, 2001b)	Fig. 3	1 adult
Chicoreus (Triplex) banksii (Sowerby, 1841)	Recent (Australia)	Houart (*Novapex*, 2001b)	Fig. 4	1 adult
Chicoreus (Triplex) axicornis (Lamarck, 1822)	Recent (Thailand)	Houart (*Novapex*, 2001b)	Fig. 5-6	2 adults
Murex tribulus (Linnaeus, 1758)	Recent (East Asian)	Merle (*Novapex*, 2001)	Fig. 9D	1 adult
Murex hystricosus Houart, 2001	Recent (Java)	Houart & Dharma (*Novapex*, 2001)	Fig. 1	1 adult
Hexaplex cichoreum (Gmelin, 1791)	Recent (Philippines)	Merle (*Novapex*, 2001)	Fig.10F	1 adult

Subfamily MURICOPSINAE

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Favartia (s.s.) brevicula (Sowerby, 1834)	Recent (Mauritius Island)	Merle (*C.R. Palevol*, 2002)	Fig. 1A	1 adult
		Merle (*Novapex*, 2001)	Fig. 17A	
Favartia (s.s.) paulmieri Houart, 2002	Recent	Houart (*Novapex*, 2002a)	Fig. 1	1 adult

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Favartia (Murexiella) bidalgoi (Crosse, 1869)	Recent (Florida, USA)	Merle (*C.R. Palevol*, 2002) Merle (*Novapex*, 2001)	Fig. 1B Fig. 17F	1 adult
Favartia (s.s.) alveata (Kiener, 1842)	Recent (Mexico)	Merle (*C.R. Palevol*, 2002) Merle (*Novapex*, 2001)	Fig. 1C Fig. 17B	1 adult
Favartia (s.s.) marianae Houart, 2003	Recent (Mozambique)	Houart (*Novapex*, 2003c)	Fig. 1	1 adult
Favartia (s.s.) conleyi Houart, 1999	Recent (New Caledonia)	Houart (*Novapex*, 2003c)	Fig. 2	1 adult
Favartia (s.s.) cecalupoi	Recent (Somalia)	Houart (*Novapex*, 2003c)	Fig. 3	1 adult
Pygmaepterys germainae (Vokes & d'Attilio, 1980)	Recent (Colon, USA)	Merle (*Novapex*, 2001)	Fig. 17C	1 adult
Maxwellia gemma (Sowerby, 1879)	Recent (California, USA)	Merle (*Novapex*, 2001)	Fig. 17D	1 adult
Pazinotus sibogae (Schepman, 1911)	Recent (Coral sea)	Merle (*Novapex*, 2001)	Fig. 17E	1 adult
Eofavartia frondosa (Lamarck, 1803)	Lutetian (France)	Merle (*C.R. Palevol*, 2002)	Fig. 1D	1 adult
Eofavartia mantelli (Conrad, 1834)	Bartonian (Alabama, USA)	Merle (*C.R. Palevol*, 2002)	Fig. 1E	1 adult
Eofavartia marchandi (Cossmann, 1903)	Lutetian (France)	Merle (*C.R. Palevol*, 2002)	Fig. 1F	1 adult
Homalocantha heptagonata (Bronn, 1831)	Burdigalian (France)	Merle (*C.R. Palevol*, 2002)	Fig. 2	1 adult
Homalocantha scorpio (Linnaeus, 1758)	Recent (Australia)	Merle (*Novapex*, 2001)	Fig. 10B,E	1 adult
Homalocantha melanomathos (Gmelin, 1789)	Recent (Cuba)	Merle (*Novapex*, 2001)	Fig. 10C	1 adult
Murexsul elatospira (Cossmann & Peyrot, 1924)	Chattian (France)	Merle (*Novapex*, 2001)	Fig. 13A-F, 14A-F	6 spm, young to adult
Murexsul oxytatus (Smith, 1938)	Recent (Virgin Island, USA)	Merle (*Novapex*, 2001)	Fig. 16A	1 adult
Murexsul cevikeri (Houart, 2000)	Recent (Turkei)	Houart (2001a)	Fig. 113	4 spm, young to adult

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Murexsul octogonus (Quoy & Gaimard, 1833)	Pleistocene (New-Zealand)	Merle (*Novapex*, 2001)	Fig. 16B	1 adult
Xastilia kosugei (Bouchet & Houart, 1994)	Recent (SW Pacific)	Merle (*Novapex*, 2001)	Fig. 16C	1 adult
Muricopsis cristata (Brocchi, 1814)	Pliocene (France, Italia)	Merle (*Novapex*, 2001)	Fig. 15A-B	2 spm, adult
Muricopsis deformis (Reeve, 1846)	Recent (Costa Rica)	Merle (*Novapex*, 2001)	Fig. 15C	1 adult
Muricopsis haideri Houart, 2003	Recent (Senegal)	Houart (*Novapex*, 2003b)	Fig. 1	1 young
Acanthotrophon carduus (Broderip, 1833)	Recent (Cantadora Island)	Merle (*Novapex*, 2001)	Fig. 15D	1 adult

Subfamily TYPHINAE

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Typhis tubifer (Bruguière, 1792)	Lutetian (France)	Merle (*Novapex*, 2001)	Fig. 11A-F	3 spm young to adult
Typhis horridus (Brocchi, 1814)	Pliocene (Italia)	Merle (*Novapex*, 2001)	Fig. 12A-B	1 adult
Monstrotyphis tosaensis (Azuma, 1960)	Recent (Japan)	Merle (*Novapex*, 2001)	Fig. 12C	1 adult
Monstrotyphis montfortii (A. Adams, 1863)	Recent	Houart (*Venus*, 2002c)	Fig. 1	1 adult

Subfamily TROPHONINAE

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Scabrotrophon inspiratum Houart, 2003	Recent	Houart (*Nautilus*, 2003a)	Fig. 1	1 adult
Scabrotrophon scarlatoi Houart, 2003	Recent	Houart (*Nautilus*, 2003a)	Fig. 2	1 adult
Trophon geversianus (Pallas, 1774)	Recent (Magellan Strait)	Merle (*Novapex*, 2001)	Fig. 12D-E	1 adult
?Trophonopsis peregra (Beyrich, 1854)	Rupelian (France)	Merle (*Annales de Paléontologie*, 2003)	Figs 2, 3	4 adults

Subfamily OCENEBRINAE

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Ocenebra erinaceus (Linnaeus, 1758)	Recent (France)	Merle (*Novapex*, 2001)	Fig. 18A, D	1 adult
Ocenebra inornata (Récluz, 1851)	Recent	Houart & Sirenko (*Ruthenica*, 2003a)	Fig. 1	1 adult

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Nucella lapillus (Linnaeus, 1758)	Recent (France)	Merle (*Novapex*, 2001)	Fig. 18B, E	1 adult
Trochia cingulata (Linnaeus, 1771)	Recent (South-Africa)	Merle (*Novapex*, 2001)	Fig. 18C, F	1 adult
Vaughtia squamata Houart, 2003	Recent (Senegal)	Houart (*Novapex*, 2003b)	Fig. 12	1 adult

Subfamily ERGALATAXINAE

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Orania archea (Houart, 1995	Recent (Philippines)	Merle (*Novapex*, 2001)	Fig. 19A-B	1 adult
Orania dharmai (Houart, 1995)	Recent (Borneo)	Merle (*Novapex*, 2001)	Fig. 19C	1 adult
Spinidrupa euracantha (Adams, 1853)	Recent (Tahiti)	Merle (*Novapex*, 2001)	Fig. 19D	1 adult
Muricodrupa fenestrata (Blainville, 1832)	Recent (New-Caleodonia)	Merle (*Novapex*, 2001)	Fig. 19E	1 adult
Ergalatax obscura (Houart, 1996)	Recent (Djibouti)	Merle (*Novapex*, 2001)	Fig. 19F	1 adult

Subfamily RAPANINAE

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Stramonita armigera (Link, 1807)	Recent (Tahiti)	Merle (*Novapex*, 2001)	Fig. 20A	1 adult
Thaisella foliacea (Conrad, 1837)	Recent (Tahiti)	Merle (*Novapex*, 2001)	Fig. 20B	1 adult
Morula granulata (Duclos, 1832)	Recent (Fiji)	Merle (*Novapex*, 2001)	Fig. 20C	1 adult
Morula angulata (Sowerby, 1893)	Recent (Mauritius)	Houart (*Novapex*, 2002b)	Fig. A	1 adult
Morula echinata (Reeve, 1846)	Recent (Guam)	Houart (*Novapex*, 2002b)	Fig. B	1 adult
Morula albinigra Houart 2002	Recent (Guam)	this paper	Fig. 1A	1 adult
Morula nodicostata (Pease, 1868)	Recent (Tahiti)	this paper	Fig. 1B	1 adult
Morula cernohorskyi (Houart & Tröndle, 1997)	Recent (Tuamotu)	this paper	Fig. 1C	1 adult
Morula parva (Reeve, 1846)	Recent (Indonesia)	this paper	Fig. 1D	1 adult

TAXA	RANGE	AUTHORS (REVIEW)	FIGURES	OBSERVATIONS
Morula variabilis (Pease, 1868)	Recent (Tuamotu)	this paper	Fig. 1E	1 adult
Drupa morum (Röding, 1798)	Recent (Mariana Island)	Merle (*Novapex*, 2001)	Fig. 20D	1 adult
Drupina glossularia (Röding, 1798)	Recent (Fiji)	Merle (*Novapex*, 2001)	Fig. 20E	1 adult